

Eggs per Recruit as a Management Indicator for the Canadian Lobster Fishery

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2006

**Canadian Technical Report of Fisheries
and Aquatic Sciences No. 2655**

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Cat. No. Fs 97-6/2655E

ISSN 0706-6457

Correct citation for this publication:

Miller, R.J. and C.G. Hannah. 2006. Eggs per recruit as a management indicator for the Canadian lobster fishery. Can. Tech. Rep. Fish. Aquat. Sci. 2655: iii + 14p.

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ABSTRACT

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Spatial correlations between eggs per recruit and fishery yields were investigated for 13 lobster fishing areas in eastern Canada in order to evaluate eggs per recruit as a management measure. Correlations were found to be negative. They were also negative after adjusting for possible larval drift between hatching and settling areas. This finding raises questions about the use of a single value of eggs per recruit in management strategies for diverse populations. Low fishery yields can lead to high values of eggs per recruit if fishers fish less hard, remove a smaller fraction of the stock, and allow individual females to live longer to produce more eggs. If management targets based on egg production are area-specific they can accommodate differences in survival from eggs to fishery recruits.

RÉSUMÉ

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Nous avons examiné la corrélation spatiale entre le nombre d'oeufs par recrue et le rendement de la pêche pour 13 zones de pêche du homard de l'est du Canada dans le but d'établir si le nombre d'oeufs par recrue peut servir de mesure de gestion. Les corrélations étaient négatives. Elles l'étaient également après ajustement pour la dérive éventuelle des larves entre les zones d'éclosion des oeufs et les zones d'établissement des larves au fond. Cette constatation soulève des questions quant à l'utilisation d'un nombre unique d'oeufs par recrue dans les stratégies de gestion de populations diversifiées. Un rendement de pêche faible peut donner un nombre élevé d'oeufs par recrue si les pêcheurs pêchent moins intensément, prélèvent une fraction plus petite du stock et permettent aux femelles de vivre plus longtemps de sorte à ce qu'elles puissent produire plus d'oeufs. Si les cibles de gestion reposant sur la production d'oeufs sont taillées sur mesure des zones, elles peuvent tenir compte des différences dans la survie des oeufs jusqu'au recrutement du homard à la pêche.

INTRODUCTION

Management measures for the American (*Homarus americanus*) and spiny (*Panulirus* sp.) lobster fisheries are commonly based on the ratio from fished and unfished populations of either egg production or eggs per recruit. Eggs per recruit (E/R) estimates the number of eggs, on average, that a single female produces in a lifetime. In a heavily fished population the average female lives to reproduce fewer times and at smaller sizes than in a lightly fished population. The United States adopted an E/R ratio of 10% as a threshold beyond which the American lobster was considered to be overfished (NEFMC 1991). In Canada, a government advisory council recommended a ratio of 5% as a target (FRCC 1995). For spiny lobster (*Panulirus* sp.) fisheries, overfishing thresholds were defined as E/R ratios of 20% for the United States Caribbean and Hawaiian Islands and 5% plus three consecutive years of declining recruits to the fishery for the southeastern United States (Rosenberg et al. 1994; DiNardo and Wetherall 1999). A ratio of 20% of spawning stock biomass was adopted as a target for the Western Australian rock lobster fishery because, historically, this level provided adequate recruitment (Caputi et al. 1996). Using a 21-year time series for southern Newfoundland, Ennis and Fogarty (1997) calculated that recruitment would balance total mortality when egg production was 2.5% of the unfished level. Applying the same method to 91 data sets on finfish from the North Atlantic, Mace and Sissenwine (1993) found the equilibrium level ranged from 2.5 to 65% and averaged ~30%. Abalone fisheries have been managed to ratios ranging from 25-50% (McShane 1995).

The purpose of this study is to examine the inter-relation of E/R and landings among areas in order to address whether the use of a single value of E/R is appropriate to the management of the American lobster fishery in Canada. E/R and fishery yields were compared for 13 fishing areas (Fig. 1), which have a combined fishing grounds of 18,000 km² and support 5000 licenses landing 22,000 t in 2000. Comparisons were made with and without correction for possible larval drift between areas. Because fishery dependent data have a high variance and risk of bias, large data sets were employed and questions were addressed with more than one data treatment.

METHODS

E/R values were calculated using the Idoine-Rago model (Anon. 1996), which is a modification of a model developed by Fogarty and Idoine (1988). Fishing mortalities were based on Leslie analysis (Ricker 1975) when suitable data were available, or the proportions of the commercial catch in successive molt classes (i.e. the reduction due to fishing plus natural mortality) (Cobb and Caddy 1989). Where these methods were compared the results were similar, although the Leslie method gave higher mortalities for eastern Nova Scotia (Tremblay and Eagles 1996) and the molt class method higher mortalities for the southern Gulf of St. Lawrence (DFO 1996). Annual natural mortality was assumed to be 15% for the lobsters that molted and 10% for those that didn't. Data sources for E/R are listed in Table 1.

Table 1. Data sources.

Data type	Areas	Sources
Egg/recruit, catch size frequencies and instantaneous fishing mortalities (F)	23-26B	Lanteigne et al. (1998), M. Mallet (Dept. Fisheries and Oceans, Moncton, New Brunswick, pers. comm. 2001)
	27-30	Tremblay and Eagles (1998)
	31-33	DFO (1998a)
Fishing area (km ²)	23-26B	J. LeGault (Dept. Fisheries and Oceans, Moncton, New Brunswick, pers. comm. 2001)
	27-32	Pringle and Duggan (1985)
	33	authors

Fishery yields were expressed as annual landings per km² of fishing ground and per km of shoreline, standard methods for comparing landings over large areas (Harding et al. 1983; Hudon 1994). Because annual exploitation rates are high at 40-75%, and all grounds with commercial densities of lobster are thought to be fished (personal observations of the responsible lobster biologists M. Lanteigne, M.J. Tremblay, and R.J. Miller), annual landings are considered a reasonable index of annual lobster production. Over a range of exploitation rates from 75% to 40% yield per recruit increases by a moderate 25% and 15% for males and females respectively (Campbell 1985), i.e. the production per recruit is about 20% higher at the lowest than at the highest exploitation rate. The areas of the fishing grounds were obtained by asking fishermen for the locations where they set traps. Maximum fishing depths ranged from 27 to 70 m. There was no measure of the quality of fishing grounds. The eastern portion of Area 33E (near the city of Halifax) and associated landings were removed because landings are known to be greatly under-reported (S.C. Nolan, unpub., Dept. Fisheries and Oceans, Dartmouth, Nova Scotia, 1996). Length of coast was measured on charts of similar scales and the methodology was consistent across areas.

Larval drift estimates were based on assumptions that the larval season spanned late June through early September (Scarratt 1964; Harding et al. 1982; DiBacco and Pringle 1992; Miller 1997; Miller et al. 2006) and most hatching occurred in depths less than 10 m. Ugarte (1994), working in the eastern part of Area 31, found that 166 of 215 ovigerous females were centered around 8 m depth and the remainder around 13 and 23 m near the time of hatching. Unpublished tagging studies in Area 32 (J.D. Pringle and R.E. Duggan, Dept. of Fisheries and Oceans, Dartmouth, Nova Scotia) and 33E (R.J. Miller) collected lobsters from 4-27 m and 4-40 m respectively. In June, near the hatching season, all 29 ovigerous females captured were taken from 4-8 m. When the appropriate larval development rates (MacKenzie 1988) were chosen for the temperature regimes in areas 23-27S (Petrie et al. 1996a) and areas 29-33W (Petrie et al. 1996b), times in the water column approximated 26 d and 34 d respectively

Net surface drift in km/d for each of the five areas in the Gulf of St. Lawrence was inferred from the results of drift bottle (surface) and current meter (30 m) information presented in Lauzier (1965) and Gregory et al. (1989). Drift for areas 27-33 was based on 3-d numerical models for mean summer (July-August) circulation in the Scotian Shelf region (Hannah et al. 2001; Han and Loder 2003), forced by observational wind stress, water density and tidal elevation data. Particle tracking simulations were conducted for release positions on a 10 x 10 km grid shoreward of the 100-m isobath, representing potential settlement positions, with the particles tracked backwards in time for the approximate duration of the larval period. This provided estimates of the hatching locations and of the probabilities of hatching in various coastal areas contributing to settlement in each area. The simulations were carried out for larvae drifting passively in the upper 1 m, upper 5 m and at 10 m, and the probabilities for the 0-1 m and 10 m cases were averaged for use in the subsequent analysis. Because of differences in the Hannah et al. (2001) and Han and Loder (2003) flow fields that are considered to be within the natural variability in the ocean, and of the focal zones for the models being the western and eastern Scotian Shelf respectively, a weighted combination of the results from the two models was used (1/0 for area 33; 0.5/0.5 for 29 and 31-32; and 0/1 for 27 and 30). No allowance was made for larval behavior that might alter the drift.

Annual egg production per km² in each area (E_A) was calculated as eggs per recruit times female recruits per km², where the subscript "A" denotes an area-specific value

$$E_A = (E/R)_A R_A$$

This calculation assumed that the number of eggs produced by one cohort of females over their mature years (the basis for the E/R calculation) is the same as the number produced by mature females of all cohorts in one year. The annual sum of eggs produced by all ovigerous females in an area would have been the preferred measure of egg production, but we have no measure of the number of ovigerous females.

R_A , the number of females in an area that recruit to fishable size in 1 year, was calculated from size frequency samples of the catch and expanded to the total landings.

$$R_A = \frac{\sum (W_{Si} / W_S) (W_L / W_{Fi})}{C}$$

The ratio of the sample weight of females in a single mm size class (W_{Si}) to the total sample weight (W_S) multiplied by the weight of annual landings in an area (W_L) gives the landed weight per mm size class. Dividing by the weight per female in a mm size class (W_{Fi}) gives the number of females landed in each size class. The total number of recruits in an area was obtained by summing over all sizes of females in a cohort and dividing by C , the fraction of the stock captured annually by the fishery. Data sources for size frequencies are given in Table 1.

A new egg production, adjusted for drift, was calculated for each receiving area as a weighted average of egg production (E_{AS} in $\text{km}^{-2}\text{yr}^{-1}$) from two or more supplying areas, where the weights (W_{AS}) were determined by the probability of drift from the supplying areas. The drift-adjusted $(E/R)_{Ar}$ for the receiving area was this number of eggs divided by the number of female recruits R_{Ar} in the receiving area.

$$(E/R)_{Ar} = \frac{\sum W_{AS} \cdot E_{AS}}{R_{Ar}}$$

This procedure was repeated using egg production (E_{AS}) and recruits (R_{Ar}) per km of shore rather than per km^2 of fishing ground.

Correlations between annual fishery yields and E/R were made for the 13 areas where fishery yields were expressed as landings in t/km^2 of fishing ground or t/km of shore. All correlation coefficients (r) were significant at the 0.05 level and all correlations except those in Fig. 2 were based on exponential (semilog) plots. Data for most correlations are listed in Table 2.

Table 2. Data used in correlations.

Area	Eggs per recruit			Landings 94-97 (t)		Female recruits		F
	No drift	Drift (km^{-1})	Drift (km^{-2})	km^{-1}	km^{-2}	km^{-1}	km^{-2}	
23	350	-	-	15.8	0.9	22200	1290	1.4
24	190	190	160	22.9	1.9	40000	3350	1.4
25	350	560	470	10.8	0.8	10000	750	1.4
26A	360	360	240	9.1	1.9	10400	2200	1.2
26B	660	800	230	6.4	2.8	7200	3100	1.4
27N	870	850	640	6.5	2.5	6900	2600	1.3
27S	1900	1370	2090	6.7	1.4	5400	1100	0.55
30	4700	4910	4240	1.9	0.8	1300	580	0.54
29	3350	5550	4770	0.6	0.3	500	230	0.50
31	4800	8070	7590	0.8	0.3	400	140	0.55
32	900	1020	1320	1.5	0.3	1100	230	0.80
33E	500	660	600	2.1	0.7	700	230	1.1
33W	500	440	420	6.2	1.6	2100	550	1.1

E/R would preferably be calculated for the same years in each area and plotted against fishery yield years later using the appropriate time lag from hatching to fishable size. However, most inputs for the E/R model (growth, fecundity, natural mortality, size at maturity) have not been measured in the same

years among areas, or even all in the same years in one area. It is usually assumed these parameters change little from year to year (Campbell 1985, Fogarty and Idoine 1988, sources in Table 1). The input that has been measured frequently, fishing mortality, has not changed markedly in two decades (Campbell and Robinson 1983; Miller et al. 1987; Tremblay and Eagles 1998; Lanteigne et al. 1998; DFO 1998a).

RESULTS

Fished E/R was used instead of the ratio of fished to unfished E/R because these two parameters were highly correlated ($r = 0.92$, Fig. 2) and because calculating unfished E/R required guesses for data on growth, fecundity, and mortality of the large females that no longer exist in most lobster stocks. The high correlation was obtained because among the 13 study areas unfished E/R varied much less than fished E/R.

Whereas fishery landings have changed over time, the relative landings among the 13 areas have not changed a great deal. That is, the high areas remained high and the low areas remained low (Fig. 3). Consequently, the time interval chosen should not greatly alter the correlations between landings and E/R, providing the years were the same for all areas. Mean landings for 1994-1997 were used unless otherwise noted.

The relationship between landings and E/R among the 13 areas was found to be negative whether yields were per unit distance of shoreline (t/km) or per unit area of fishing ground (t/km²) (Fig. 4). Mean landings per km of shoreline for the 1970s and 1980s were also plotted against E/R with similar negative results (Fig. 5). If we are correct that the inputs used to calculate E/R are stable over time and that landings maintain positions of relative abundance, then these results indicate areas with high E/R do not necessarily or even generally have high landings.

Fig. 1 includes the probabilities that larvae were hatched in the area of settlement or drifted in from either side. These probabilities were used to generate the drift-adjusted E/R for each area. The net drift in the area of study is east past both sides of Prince Edward Island, south along the eastern end of Nova Scotia, then west along the outer coast of Nova Scotia (Bumpus and Lauzier 1965; Han et al. 1999). However, as shown for Areas 33 E, 32, and 31, there can be local and/or temporary reversals of this flow on the outer coast during the summer larval period (also see Petrie et al. 1987 and Greenberg et al. 1997). In area 31 drift adjusted E/R increased over the no drift value (Table 2) because egg density was quite high in upstream areas 30 and 27S and there were a relatively small number of recruits in Area 31 over which to distribute the increased egg production.

Fig. 6 shows the landings plotted against the E/R adjusted for larval drift. The negative correlations remain, and are a little stronger (c.f. Fig. 4). Drift rates are uncertain because few measurements have been taken near shore and the models used here have limited resolution of nearshore features. However, for the correlations in Fig. 6 to become positive, the larvae from the three areas with the highest E/R, Areas 29, 30, and 31 (the points to the right in Figs. 4 and 6) must drift to areas of high landings. The six areas with highest landings in t/km are all upstream, and five of the six areas in t/km² are upstream, mostly in the Gulf of St. Lawrence. This movement is unlikely given that the mean flow is generally directed out of the Gulf of St. Lawrence around Cape Breton and to the southwest along the inner Scotian Shelf (Han et al. 1999; Hannah et al. 2001).

What mechanism could cause E/R and fishery yields to be negatively correlated? Where lobster density and annual recruitment to the fishery are low, we hypothesise that fishers remove a lower fraction of legal biomass before reaching a catch level giving unacceptable economic return. Clark (1985) calls this stock size the bionomic equilibrium. As a result of the lower rate of exploitation, the average female survives longer, reproduces more times, and E/R is higher. The observed negative spatial correlation can occur where the fishery has underused fishing capacity and effort is not constrained by catch quotas, i.e. the available fishing time does not limit the catch.

Evidence that exploitation rate is related to annual yield is supported by positive correlations between F and landings in either t/km^2 ($r = 0.65$) or t/km ($r = 0.80$). Finally, the highest weekly average catch per trap haul is also a measure of yield and is positively correlated with F ($r = 0.68$). Catches per trap haul were obtained from fisher's log books (Tremblay and Eagles 1996; Lanteigne et al. 1998, Miller and Duggan 2004).

DISCUSSION

Spatial correlations of egg per recruit versus landings were negative with or without adjustment for larval drift. Neither variable needs to be measured with high precision to obtain a significant correlation because the highest value of E/R was 25 times the lowest, and the highest landings per unit area was 10 times the lowest.

The sign of these correlations is the opposite to that implied by the use of a single E/R target value across diverse areas in lobster fisheries management. Four possibilities why positive correlations between E/R and landings were not obtained are as follows:

1. The many inputs required to calculate lobster E/R (Campbell 1985) provide ample opportunity for error. However, improbably large changes would be needed to reverse the correlations from negative to positive. Calculating E/R as a percentage of the unfished level, as used for some management targets, was not used here because of uncertainties in data on the rare (or non-existent) large females. Also, the ratios (as uncertain as they are) were highly correlated with E/R .
2. E/R is calculated per female and is not necessarily a good analogue of population egg production. As described above, a low stock density can lead to low fishing mortality and longer survival of females which in turn gives a high E/R . This hypothesis is consistent with Beverton's (1998) view that management targets based on per recruit fail to address stock stability and hence risk stock collapse.
3. Egg production and fishery yield can be uncoupled if larval drift separates the areas where larvae hatch from where lobsters recruit to the fishery. However, adjusting E/R for plausible speeds and directions of drift did not result in a positive correlation with landings.
4. Egg production and fishery yield can also be uncoupled if benthic stage lobsters migrate long distances between the times they settle to the bottom and are taken by the fishery. Extensive lobster tagging throughout the 13 areas of this study has shown little movement between areas (Campbell 1989; Miller et al. 1989; Tremblay et al. 1998; Comeau et al. 1999). Most movement is short-distance seasonal migration.

Applying a single E/R management target to a large area, such as the entire Canadian fishery (FRCC 1995), presumes that survival from hatching to recruitment to the fishery is spatially uniform or that the value is set conservatively enough to provide good recruitment to the stock with the lowest survival. Meeting the second assumption could require very high E/R values. For example, area 31 had the highest E/R but landings at only 10% of historic highs, whereas area 24 with the lowest E/R (5% of that in LFA 31) had historically high catches (Table 2)(Miller 2003).

Spatially uniform survival to recruitment is unlikely. Table 3 and Fig. 7 summarize survival of pelagic lobster stages for Canadian studies where sampling was adequate. These data are annual production of post-larvae at the time of settling as a percentage of stage I annual production. All sampling was with neuston nets and production was calculated as in Scarratt (1963). Sampling biases existed (Miller et al. 2006) but were probably similar among studies. There was no adjustment for larval drift, but one can see in Table 2 that changes in E/R with and without adjustment for drift are smaller than differences in survival. The data for the Magdalen Islands (the northern most data in Fig. 7) may be an exception as

significant numbers of PL may have recruited from upstream (Hudon et al. 1986) of the survey area of Ouellet et al. (2001). The "high" and "low" values in western Nova Scotia are based on indices of ovigerous female and post-larval density but annual production could not be calculated. The data in Table 3 and Fig. 7 indicate large spatial and temporal variation in survival of pelagic stages.

Table 3. Studies giving survival of lobster pelagic stages. Mean values are mapped near the study sites in Fig. 7.

Annual survival (%)		No. years	Source
Mean	Range		
0.9	0.1-2.5	15	Scarratt (1964, 1973)
3.5	1.7-5.0	3	Ouellet et al. (2001)
2.7	1.6-4.0	3	Miller et al. (2006)
2.5	1.3-3.2	3	"
0.05	0-0.09	3	"
2.5	-	1	Harding et al. (1982)
0.15	0.13-0.17	2	Miller (unpub.)
0.15	0-0.31	2	"
0	-	1	Dibacco and Pringle (1992)
low	-	2	Miller (1997)
high	-	2	"

Post-larval densities in Rhode Island (Fogarty 1983; Incze et al. 1997), New Hampshire (Fogarty 1983; Incze et al. 2000), Massachusetts (Fogarty 1983), and Maine (Incze et al. 2000) were nearly always greater than in Canadian studies. Abundance of post-larvae was often greater than that of stage I (Fogarty 1983) providing improbably high survival rates.

Food, predators, temperature, or drift to areas unfavorable for settlement can affect the quality of pelagic habitat and survival (Ennis 1995). Robinson (1979) suggested that different spawner-recruit relationships between the southern Gulf of St. Lawrence and the outer coast of Nova Scotia were due to lower larval survival on the outer coast. A Nova Scotia study suggested survival of *H. americanus* larvae varied widely over a spatial scale of only 200 km (Miller 1997). However, in spiny lobster fisheries that share a common pool of larvae (Phillips 1981), spatial differences in larval survival may be unimportant.

E/R can be a useful measure for lobster management strategies and evaluations because it can be used to calculate relative benefits of different fisheries regulations. Also, the typical level of <2% of unfished egg production in Canada (DFO 1998 a, b, c, d) appears low and has provided a direction for improvement. It may be a useful stock-specific measure of health if one knows the stock boundaries and has a reliable time series of E/R and fishery yield, and if the conditions relating E/R to stock egg production do not change.

The negative spatial correlation found between E/R and lobster yield, and the possibility that observed values of E/R result from fishers' behavior responding to the economics of fishing, suggest a single E/R target is not suitable for a large area. Fishery managers and fishery scientists are put in an awkward position when areas experiencing near record catches have low E/R values and areas with historically depressed catches have the highest E/R. Apparently, different areas require widely dissimilar numbers of eggs to make a recruit lobster.

ACKNOWLEDGEMENTS

We thank the Prince Edward Island Department of Fisheries, Agriculture and Environment and the Guysborough County Inshore Fishermen's Association for supporting the lobster larval sampling in Prince Edward Island and eastern Nova Scotia. G. Han provided circulation model fields, S. Oakey carried out the particle tracking computations, K.F. Drinkwater made suggestions for calculating E/R following larval drift, M. Mallet and M.J. Tremblay provided lobster size frequencies in the catch in Areas 23-26b and 27N-30 respectively, and J. LeGault for provided sizes of lobster fishing grounds in Areas 23-26b. J.W. Loder, M.J. Fogarty, K.F. Drinkwater, and R.K. Mohn commented on the manuscript.

REFERENCES

- Anon. 1996. 22nd Northeast Regional Stock Assessment Workshop. Northeast Fisheries Science Center Ref. Doc. 96-13, Woods Hole, MA.
- Beverton, R. (1998). Fish, fact and fantasy: a long view. *Rev. Fish. Biol. and Fish.* 8: 229-249.
- Bumpus, D.F., and L.M. Lauzier. 1965. Surface circulation on the continental shelf off Eastern North America between Newfoundland and Florida. *Serial Atlas of the Marine Environment* American Geographical Society.
- Campbell, A. 1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. *N. A. J. of Fish. Mgm.* 5: 91-104.
- Campbell, A. 1989. Interim report on dispersal of lobsters (Homarus americanus) tagged off southern Nova Scotia. *Can. Ms. Rep. Fish. Aquat. Sci.* 2022: 29 p.
- Campbell, A., and D.G. Robinson. 1983. Reproductive potential of three American lobster (Homarus americanus) stocks in the Canadian Maritimes. *Can. J. Fish. and Aquat. Sci.* 40: 1958-1967.
- Caputi, N., C. Chubb, N. Hall, and A. Pearce. 1996. Relationships between different life history stages of the western rock lobster, Panulirus cygnus, and their implications for management. *In* *Developing and Sustaining World Fisheries Resources, the State of Science and Management* (D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer eds.) p. 579-585, CSIRO, Canberra, Australia.
- Clark, C.W. 1985. Bioeconomic modelling and fisheries management. Wiley, New York.
- Cobb, J.S., and J.F. Caddy. 1989. The population biology of decapods. *In* *Marine Invertebrate Fisheries, Their Assessment and Management* (J.F. Caddy, ed.) p. 327-374. John Wiley and Sons: London.
- Comeau, M., M. Lanteigne, G. Robichaud, and F. Saovie. 1999. Lobster (Homarus americanus) movement in the southern Gulf of St. Lawrence – summary sheets of tagging projects conducted between 1980 and 1997. *Can. Ind. Rep. Fish. and Aquat. Sci.* 249: 111 p.
- Dibacco, C., and J.D. Pringle. 1992. Larval lobster (Homarus americanus, H.Milne Edwards, 1837) distribution in a protected Scotian Shelf Bay. *J. Shellfish Res.* 11: 81-84.
- DFO. 1996. American lobster (Homarus americanus), Southern Gulf of St. Lawrence. Department of Fisheries and Oceans Science Stock Status Report 96/115E, 7 p.
- DFO. 1998a. Eastern and South Shore Nova Scotia lobster LFAs 31-33. Department of Fisheries and Oceans Science Stock Status Report C3-60, 7 p.

- DFO. 1998b. Eastern Cape Breton lobster (LFAs 27-30). Department of Fisheries and Oceans Science Stock Status Report C3-59, 6 p.
- DFO. 1998c. Southern Gulf of St. Lawrence lobster (LFAs 23, 24, 25, 26A, and 26B). Department of Fisheries and Oceans Science Stock Status Report C3-12, 8 p.
- DFO. 1998d. Bay of Fundy lobster (LFAs 35, 36, and 38). Department of Fisheries and Oceans Science Stock Status Report C3-61, 8 p.
- DiNardo, G.T., and J.A. Wetherall. 1999. Accounting for uncertainty in the development of harvest strategies for the Northwestern Hawaiian Islands lobster trap fishery. *ICES J. Mar. Sci.* 56: 943-951.
- Ennis, G.P. 1995. Larval and postlarval ecology. In *Biology of the lobster, Homarus americanus*. (J.R. Factor, ed.) p. 23-46. Academic Press: New York.
- Ennis, G.P., and M.J. Fogarty. 1997. Recruitment overfishing reference point for the American lobster, *Homarus americanus*. *Mar. Freshwat. Res.* 48: 1029-1034.
- Fogarty, M.J. 1983. Distribution and relative abundance of American lobster, *Homarus americanus*, larvae: New England investigations during 1974-79. NOAA Tech. Rep. NMFS SSRF-775, 64 p.
- Fogarty, M.J., and J.S. Idoine. 1988. Application of a yield and egg production model based on size to an offshore American lobster population. *Trans. Am. Fish. Soc.* 117: 350-362.
- FRCC (Fisheries Resource Conservation Council). 1995. A conservation framework for Atlantic lobster. Publ. No. FRCC95.R.1 Canada Department of Fisheries and Oceans, Ottawa, Ont.
- Greenberg, D.A., J.W. Loder, Y. Shen, D.R. Lynch, and C.E. Naimie. 1997. Spatial and temporal structure of the barotropic response of the Scotian Shelf and Gulf of Maine to surface wind stress: a model-based study. *J. Geophys. Res.* 102: 20897-20915.
- Gregory, D.N., O.C. Nadeau, and D. Lefaivre. 1989. Current statistics of the Gulf of St. Lawrence and estuary. *Can. Tech. Rep. Hydrog. Ocean Sci.* 120: 178 p.
- Han, G. and J.W. Loder. 2003. Three-Dimensional seasonal-mean circulation and hydrography on the eastern Scotian Shelf. *J. of Geophys. Res.* 108(C5):5-1—5-21.
- Han, G., J.W. Loder, and P.C. Smith. 1999. Seasonal-mean hydrography and circulation in the Gulf of St. Lawrence and on the eastern Scotian and southern Newfoundland shelves. *J. Phys. Oceanogr.* 29: 1279-1301.
- Hannah, C.G., J.A. Shore, J.W. Loder, and C.E. Naimie. 2001. Seasonal circulation on the western and central Scotian Shelf. *J. Phys. Oceanogr.* 31: 591-615.
- Harding, G.C., W.P. Vass, and K.F. Drinkwater. 1982. Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. *Can. J. Fish. Aquat. Sci.* 39: 1117-1129.
- Hudon, C., P. Fradette and P. Legendre. 1986. La repartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des îles de la Madeleine golfe du Saint-Laurent. *Can. J. Fish. Aquat. Sci.* 43: 2164-2176.

- Incze, L.S., R.A. Wahle, and J. S. Cobb. 1997. Quantitative relationships between postlarval production and benthic recruitment in lobsters, Homarus americanus. Mar. Freshwat. Res. 48: 729-743.
- Incze, L.S., P. Aas, T. Ainaire, and M. Bowen. 2000. Neustonic postlarval American lobsters, Homarus americanus, in western Gulf of Maine: spatial and interannual variations. Can. J. Fish. Aquat. Sci. 57: 755-765.
- Lauzier, L.M. 1965. Drift bottle observations in Northumberland Strait, Gulf of St. Lawrence. J. Fish. Res. Bd. Can. 22: 353-368.
- Lanteigne, M., M. Comeau, P. Mallet, G. Robichaud, and F. Savoie. 1998. The American lobster, Homarus americanus, in the southern Gulf of St. Lawrence (Lobster Fishing Areas 23, 24, 25, 26A and 26B). Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Res. Doc. 98/72.
- Mace, P.M., and M.P. Sissenwine. 1993. How much spawning per recruit is enough? In 'Risk Evaluation and Biological Reference Points for Fisheries Management'. (Eds S.J. Smith, J.J. Hunt, and D. Rivard). Can. Spec. Publ. Fish. Aquat. Sci. 120: 101-108.
- MacKenzie, B.R. 1988. Assessment of temperature effects on interrelationships between stage durations, mortality and growth in laboratory-reared Homarus americanus. J. Exp. Mar. Biol. and Ecol. 116: 87-98.
- McShane, P.E. 1995. Recruitment variation in abalone: its importance to fisheries management. Mar. Freshwat. Res. 46: 555-570.
- Miller, R.J. 1997. Spatial differences in the productivity of American lobster in Nova Scotia. Can. J. Fish. Aquat. Sci. 54: 1613-1618.
- Miller, R.J. 2003. Be-all-you-can-be management targets for Canadian lobster fisheries. Fish. Res. 64:179-184.
- Miller, R.J. and R.E. Duggan 2004. Effects of recent management changes and stock status in lobster fishing areas 31 and 32. Canadian Science Advisory Secretariat Res. Doc. 2004/038, 40 p.
- Miller, R.J., M. Mallet, M. Lanteigne, and R. MacMillan. (in press). Bottlenecks to fishery yield for American lobster in a portion of the Gulf of St. Lawrence. N. A. J. Fish. Mgm.
- Miller, R.J., D.S. Moore, and J.D. Pringle. 1987. Overview of the inshore lobster resources in the Scotia-Fundy Region. Canadian Atlantic Fisheries Scientific Advisory Committee 97/85, Research Document, 20 p.
- Miller, R.J., R.E. Duggan, D.G. Robinson, and Z. Zheng. 1989. Growth and movement of Homarus americanus on the outer coast of Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 1716: 16 p.
- NEFMC (New England Fisheries Management Council). 1991. Amendment #4 to the American lobster fishery management plan. New England Fisheries Management Council, Saugus, Mass.
- Ouellet, P., D. Lefavre, and J.-P. Allard. 2001. Lobster (Homarus americanus) larvae abundance and post-larvae availability to settlement at the Magdalen Islands, southern Gulf of St. Lawrence (Quebec). Can. Tech. Rep. Fish. Aquat. Sci. 2328:14-18.

- Petrie, B., K. Drinkwater, A. Sandstrom, R. Pettipas, D. Gregory, D. Gilbert, and P. Sekhon. 1996a. Temperature, salinity, and sigma-t atlas for the southern Gulf of St. Lawrence. Can. Tech. Rep. Hydrogr. and Ocean Sci. 178, 256 p.
- Petrie, B., K. Drinkwater, D. Gregory, R. Pettipas, and A. Sandstrom. 1996b. Temperature and salinity atlas for the Scotian Shelf and the Gulf of Maine. Canadian Technical Report of Hydrography Ocean Sciences 147: 398 p.
- Petrie, B.D., B.J. Topliss, and D.G. Wright. 1987. Coastal upwelling and eddy development off Nova Scotia. J. Geophys. Res. 92: 12979-12991.
- Phillips, B.F. 1981. The circulation of the south eastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. 19:11-39.
- Pringle, J.D. and R.E. Duggan. 1985. Estimates of yield per unit area of fishing ground for oceanic Nova Scotia lobster districts. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 85/102, 16 p.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191: 382 p.
- Robinson, D.G. 1979. Consideration of the lobster (Homarus americanus) recruitment overfishing hypothesis, with special reference to the Canso Causeway. Can. Fish. Mar. Serv. Tech. Rep. 834, Pt. 3:78-97.
- Rosenberg, A. et al. 1994. Scientific review of definitions of overfishing in U.S. fishery management plans. U.S. Dept. Commerce NOAA Technical Memorandum NMFS-F/SPO-17, 205 p.
- Scarratt, D.J. 1964. Abundance and distribution of lobster larvae (Homarus americanus) in Northumberland Strait. Journal of the J. Fish. Res. Bd. Can. 21: 661-680.
- Scarratt, D.J. 1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962-63, and their relationships with commercial stocks. J. Fish. Res. Bd. Can. 30:1919-1824.
- Tremblay, M.J., and M.D. Eagles. 1996. Recent trends in the lobster fishery off eastern Cape Breton (LFAs 27-30: catch rate and exploitation. Department of Fisheries Atlantic Fisheries Res. Doc. 96/141: 21 p.
- Tremblay, M.J., and M.D. Eagles. 1998. Eastern Cape Breton lobster (LFA 27-30): Stock status and eggs-per-recruit-estimates. Canadian Stock Assessment Secretariat Res. Doc. 98/124, 28 p.
- Tremblay, M.J., M.D. Eagles, and G.A.P. Black. 1998. Movements of the lobster, Homarus americanus, off northeastern Cape Breton Island, with notes on lobster catchability. Can. Tech. Rep. Fish. Aquat. Sci. 2220: 32 p.
- Ugarte, R.A. 1994. Temperature and the distribution of mature female lobsters (Homarus americanus Milne Edwards) off Canso, N.S. PhD dissertation, Dalhousie University, Halifax, Nova Scotia, Canada.

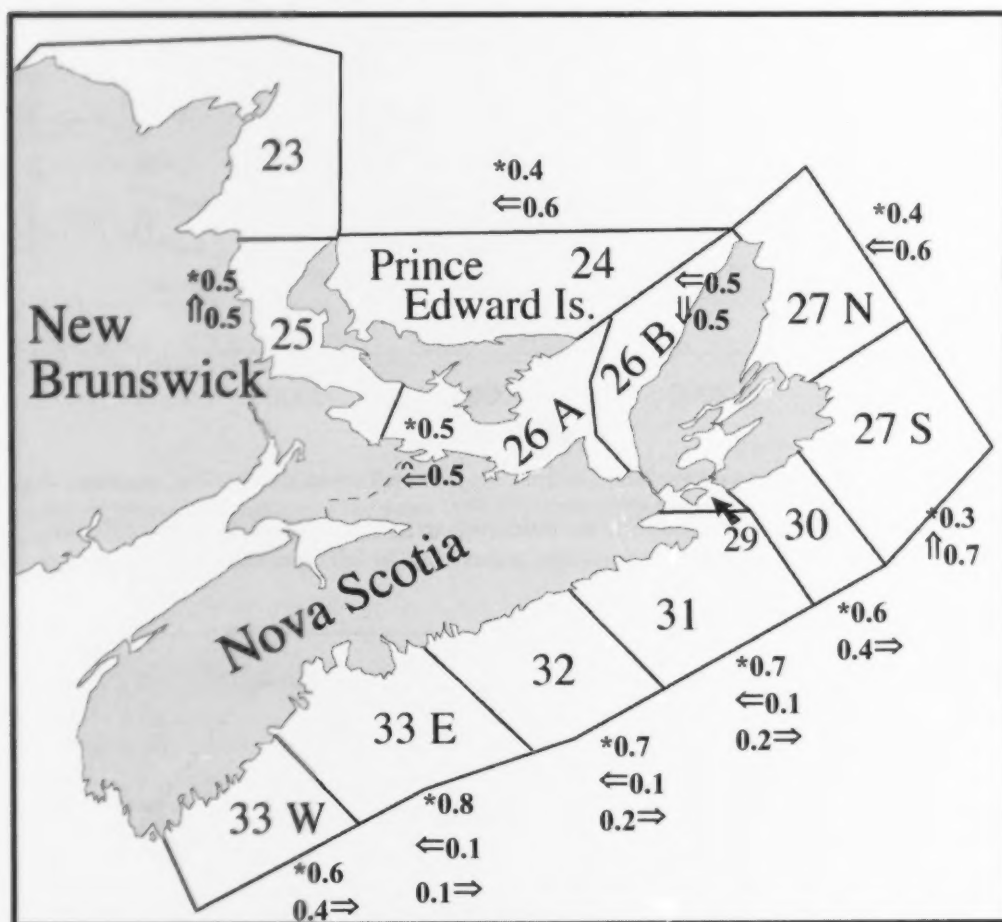


Fig. 1. Large numbers are lobster Fishing Areas in the Canadian Maritime Provinces. Small numbers with decimals points are the probabilities that larvae were hatched in the same area as settlement (*), or were hatched in areas other than the area of settlement. The symbols ⇐, ⇒, or ↑ indicate the direction of hatch.

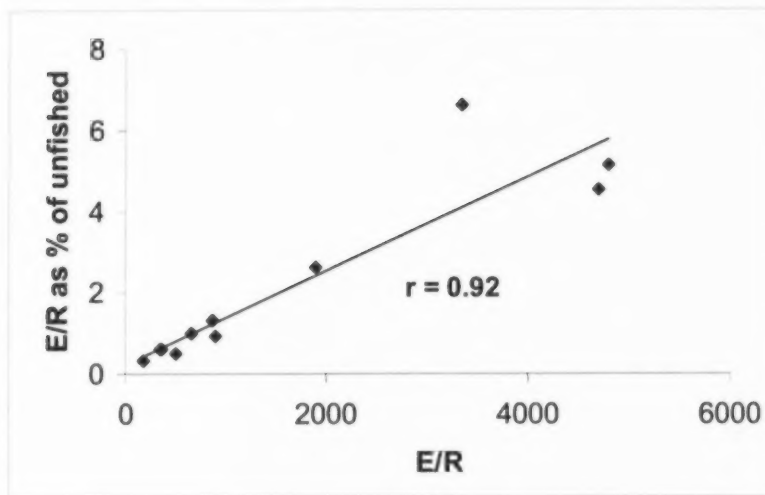


Fig. 2. Fished E/R compared to fished E/R as a percentage of unfished E/R for 13 Areas. Thirteen points are not shown because the second and third points from the left represent more than one area.

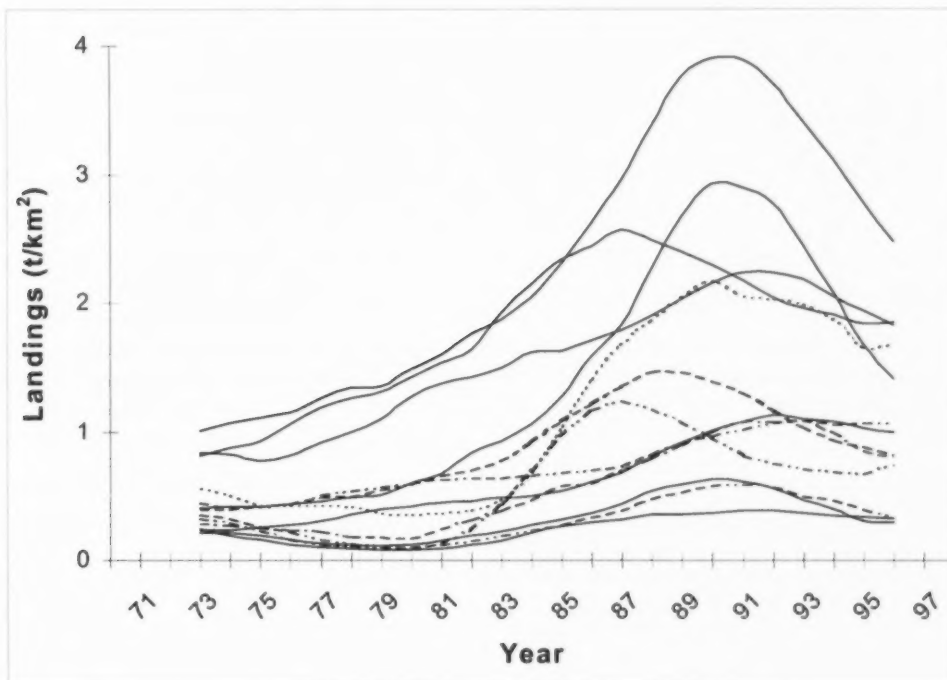


Fig. 3. Five-year running averages of annual landings from 1970-97 for 13 fishing areas.

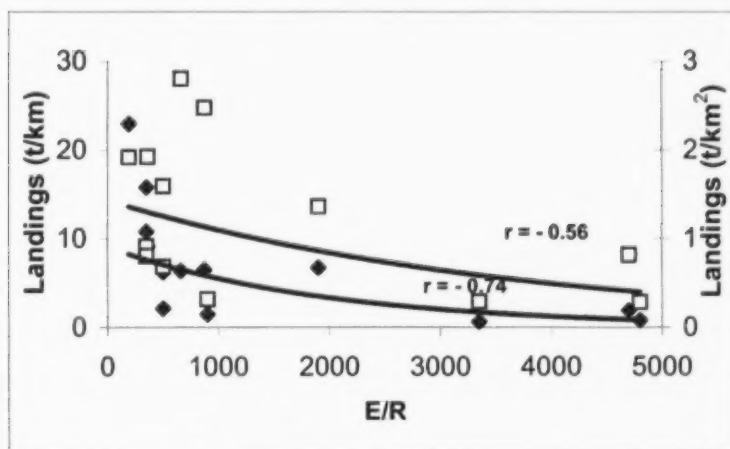


Fig. 4. Landings (solid diamonds for t/km of shore – left axis, and open squares for t/km² of fishing ground – right axis) averaged over the years 1994-97, versus eggs per recruit (E/R) for 13 fishing areas.

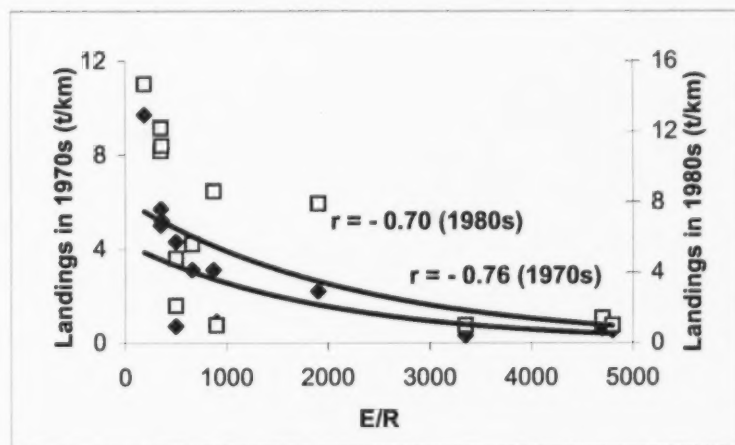


Fig. 5. Landings in t/km of shore, averaged over the years 1970-79 (solid diamond – left axis) and 1980-89 (open squares – right axis), versus eggs per recruit (E/R) for 13 fishing areas.

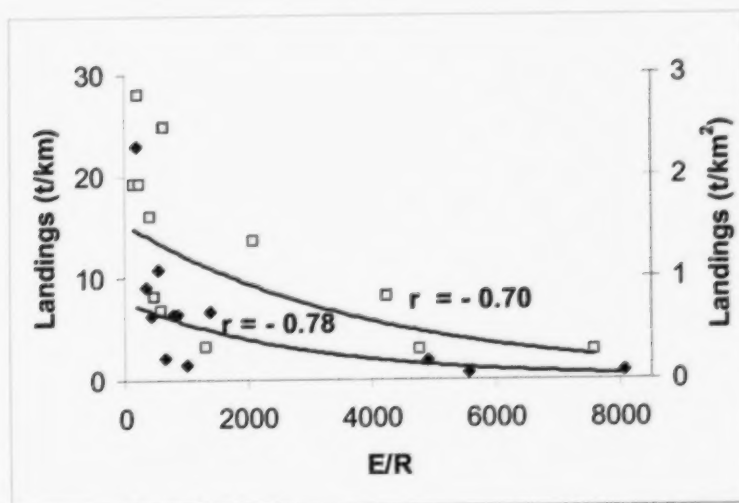


Fig. 6. Landings (solid diamonds for t/km and open squares for t/km²) averaged over the years 1994-97, versus eggs per recruit (E/R) for 12 fishing areas after allowing for drift of larvae. Area 23 was omitted because of lack of data on larval drift from upstream.

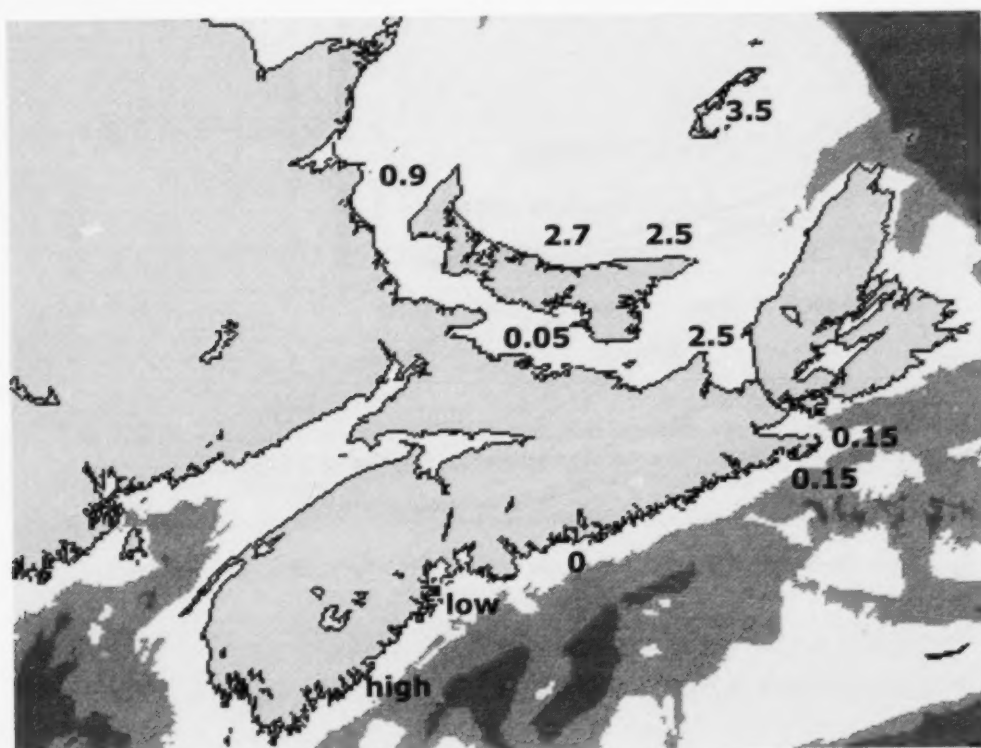


Fig. 7. Percent survival through pelagic stages for 11 locations. Details of data sources are in Table 3.

